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# Range extension of the Central American Red Brocket, *Mazama temama* (Kerr, 1792) (Artiodactyla, Cervidae), in Colombia

Héctor E. Ramírez-Chaves[1,2*], Paula Andrea Ossa-López[1], Luis Lasso-Lasso[3], Fredy A. Rivera-Páez[1], Néstor Roncancio-Duque[4], Luis A. Escobedo-Morales[5], Jesús E. Maldonado[6]

**1** Grupo de Investigación en Genética, Biodiversidad y Manejo de Ecosistemas (GEBIOME), Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Calle 65 No. 26-10, Aparatado aéreo 275; 170004, Manizales, Caldas, Colombia • HERC: hector.ramirez@ucaldas.edu.co https://orcid.org/0000-0002-2454-9482 • PAOL: paula.ossa@ucaldas.edu.co https://orcid.org/0000-0002-9079-4988 • FARP: fredy.rivera@ucaldas.edu.co https://orcid.org/0000-0001-8048-5818

**2** Centro de Museos, Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia

**3** Profesional Monitoreo Santuario de Fauna y Flora Galeras, Dirección Territorial Andes Occidentales, Parques Nacionales Naturales de Colombia, Calle 13 No. 36-56 esquina Barrio La Castellana Pasto, Nariño, Colombia • LLL: luisglasso@gmail.com

**4** Asesor en Biología de la conservación - Dirección Territorial Andes Occidentales, Parques Nacionales Naturales de Colombia, Carrera 42 # 47-21. Int. 202, Medellín, Colombia. • NRD: nroncanciod@gmail.com https://orcid.org/0000-0001-8575-8272

**5** Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, A.P.70-153, Mexico City 04510, Mexico • LAEM: laembiol@gmail.com https://orcid.org/0000-0002-8049-333X6

**6** Smithsonian Conservation Biology Institute, Center for Conservation Genomics, National Zoological Park, 3001 Connecticut Ave., NW, Washington, DC 20008, USA • JEM: maldonadoj@si.edu https://orcid.org/0000-0002-4282-1072

* Corresponding author

**Abstract**

*Mazama temama* (Kerr, 1792) is a representative species of the northern Neotropics, but the geographic range limits for this species remain unclear. We report the southernmost record of *M. temama* from the southwestern Colombian Andes, increasing the previously known range of this species by more than 300 km. We obtained a cytochrome gene sequence (849 bp) which is 95% identical to samples from Mexico. This record raises the need for extensive sampling to obtain more complete information about the distribution of *M. temama* in northern Colombia.

**Keywords**

Andes, cytochrome-b, deer, distribution, range extension

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## Introduction

Previous studies of deer diversification in the Neotropics have revealed an astonishing evolutionary history (Duarte et al. 2008). During the Great American Biotic Interchange (Woodburne 2010), a rapid diversification occurred after different deer lineages migrated into South America (Duarte et al. 2008; Escobedo-Morales et al. 2016), giving rise to 15 currently recognized deer species in that continent (Burgin et al. 2020). Recent accounts

for Colombia have listed six to 11 species included in the genera *Mazama* Rafinesque, 1817, *Odocoileus* Rafinesque, 1832, and *Pudu* Gray, 1852 (Solari et al. 2013; Montenegro et al. 2019; Burgin et al. 2020). While recent genetic studies have elucidated the complex systematics of Neotropical deer (Duarte et al. 2008; Hassanin et al. 2012; Gutiérrez et al. 2015, 2017; Escobedo-Morales et al. 2016), information on the taxonomy and distribution of cervids in Colombia remain controversial.

The Central American Red Brocket Deer, *Mazama temama* (Kerr, 1792), distributed from Mexico to northwestern Colombia (Bello-Gutiérrez et al. 2010), is restricted in its southern limit of its range to the Caribbean and Pacific regions in the departments of Chocó and Valle del Cauca (Montenegro et al. 2019). The presence of this species in the Colombian Andean region (Parque Nacional Chingaza, Cordillera Oriental) has been suggested based on genetic evidence from a specimen originally identified as *Odocoileus* (Hassanin et al. 2012) and later as *Mazama temama* (Escobedo-Morales et al. 2016; Gutiérrez et al. 2017) based on the high cytochrome-b sequence similarity with Mexican samples. Besides the efforts to clarify the distribution of *M. temama* in Colombia (Bello et al. 2016; Montenegro et al. 2019; Burgin et al. 2020), the distributional limits of this species in the country are unclear and based on limited evidence. Furthermore, there are no ecological studies of *M. temama* in Colombia (Montenegro et al. 2019), limiting national risk assesments. This also seems to be true for the global assessments which is Data Deficient due to taxonomic uncertainty (Bello et al. 2016). For those reasons, there is an increasing need for filling information gaps in the distribution of this and other deer species in Colombia, and the correct identification of specimens is crucial to document their genetic diversity in this part of their range. Here, we present a new record of *M. temama* that helps to clarify the presence of this species in northern South America.

# Methods

We obtained incidental photographs of live specimens and a skull with adherent skin and soft tissue of one adult male found shot dead. The dead-collected specimen was deposited in the Museo de Historia Natural, Universidad de Caldas (MHN-UCa), Manizales, Caldas, Colombia. We took 14 linear measurements (Table 1) of the cranium and mandible following Gutiérrez et al. (2015), including: interorbital breadth (IB), frontal length (FL), intercondylar width (IW), zygomatic breadth (ZB), palatine-premaxillary length (PPL), basal length (BL), condylobasal length (CBL), greatest length of nasals (GLN), maxillary diastema-premaxillary length (MDPL), upper tooth row length (UTRL), occipital condyle-premolar length (COPL), lower tooth row length (LTRL), notch height (NH), and jaw length (JL), as well as antler length. Measurements were taken to the nearest 0.01 mm with digital calipers.

We also extracted DNA from muscle samples with the Wizard® Genomic DNA Purification kit (Promega Corporation) following the manufacturer's instructions. Amplification of the mitochondrial cytochrome-b gene (cyt-b) was performed using the primer pair LGL765F and LGL766R, targeting a ≈1140 bp (Bickham et al. 1995, 2004). The final amplification reaction volume was 30 μL, which contained 20.24 μL ultrapure water, 3 μL 10× buffer, 0.9 μL $MgCl_2$ (50 mM), 2.4 μL dNTP mix (10 mM), 0.36 μL of each primer (25 μM), 1.2 U of Taq DNA Polymerase, and 2.5 μL DNA (approximately 110 ng of DNA). The amplification was performed on a Techne TCPLUS thermocycler: initial denaturation of 3 min at 94 °C, followed by 35 cycles of 95 °C for 45 s of denaturing, 50 °C for 40 s of annealing, 72 °C for 45 s of extension, completing the reaction with a final extension cycle at 72 °C for 7 min. The PCR products were quantified by fluorometry using a Quantus Fluorometer™ (Promega®). PCR products were sent to Macrogen Inc. (South Korea) for

**Table 1.** Cranial measurements of the new record of *Mazama temama* from Colombia. The measurements of the Neotype of *M. americana* and of several specimens of *M. rufina* were taken from Cifuentes-Rincón et al. (2020) and Gutiérrez et al. (2015), respectively.

| Measurement | *Mazama temama* MHN-UCa-M 1859 | *Mazama americana* neotype | *Mazama rufina* |
|---|---|---|---|
| Sex | Male | Male | Males and females |
| | Colombia | | Colombia–Venezuela |
| Condylobasal length (CBL) | 183.90 | 211.15 | 145.81–154.80 |
| Basal length (BL) | 170.44 | 197.73 | 136.23–149.36 |
| Zygomatic breadth (ZB) | 85.43 | 101.86 | 64.49–76.65 |
| Greatest length of nasals (GLN) | 65.45 | 70.53 | 31.51–54.09 |
| Upper tooth row length (UTRL) | 60.35 | 65.73 | 43.51–53.12 |
| Interorbital breadth (IB) | 44.77 | | 32.10–42.82 |
| Frontal length (FL) | 55.24 | | 48.63–68.48 |
| Intercondylar width (IW) | 36.34 | | 29.33–34.63 |
| Palatine-premaxillary length (PPL) | 89.03 | | 61.35–75.45 |
| Occipital condyle-premolar length (COPL) | 126.69 | | 99.26–115.12 |
| Lower tooth row length (LTRL) | 65.08 | | 48.95–57.46 |
| Notch height (NH) | 47.30 | | 30.32–38.80 |
| Jaw length (JL) | 153.84 | | 113.20–136.56 |
| Maxillary diastema-premaxillary length (MDPL) | 61.14 | | |

purification and DNA sequencing. The sequencing chromatogram was evaluated and edited with the software Geneious Prime 2020.2.4 (https://www.geneious.com; Drummond et al. 2009). We compared the edited 849 bp cyt-b sequence by performing independent searches with the Basic Alignment Search Tool (BLAST) (Altschul et al. 1990) to obtain overall similarity and downloaded sequences of closely related taxa available in GenBank (Table 2) to conduct a phylogenetic analysis. For all analyses, we used *Alces alces*, *Capreolus capreolus* Linnaeus, 1758, and *Hydropotes inermis* (Gilbert et al. 2006; Hassanin et al. 2012; Gutiérrez et al. 2017) as outgroup taxa (Table 2). We aligned sequences using default options of ClustalW (Thompson et al. 1997), included in the program MEGA X (Kumar et al. 2018). Genetic distances for cyt-b were estimated using the *p*-distance method. We selected the best-fitting models of sequence evolution, using the Akaike Information Criterion (AIC) calculated with ModelFinder (Kalyaanamoorthy et al. 2017) in PhyloSuite (Zhang et al. 2020). We conducted phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI). ML was conducted with IQ-TREE (Nguyen et al. 2015) under the TIM2+I+G4+F model for 5000 ultrafast bootstraps (Minh et al. 2013), as well as Shimodaira–Hasegawa-like approximate likelihood-ratio test (SH-like aLRT) for branches with 1000 replicates (Guindon et al. 2010), all included in PhyloSuite platform (Zhang et al. 2020). The BI was conducted in MrBayes 3.2.6 (Ronquist et al. 2012) under the GTR+F+G4 model; four parallel runs and four Markov chains were run for 15,000,000 generations and 25% of sampled data were discarded as burn-in. Finally, we used FigTree v. 1.4.3 to visualize the phylogenetic trees (Rambaut 2007).

To explore how the inclusion of the new records from Colombia determines the predicted geographic range for the species, we developed a species distribution model on MaxEnt software (Phillips et al. 2006, 2020). We searched for presence data in the Global Biodiversity Information Facility (GBIF) database (GBIF 2021), including both specimens and human observations as well as records from the literature. The resulting database was curated to remove dubious records and duplicated locations (96 unique presence records). We used the 19 WorldClim variables (Fick and Hijmans 2017) at 2.5 arc-minutes resolution and delimitated a buffer area of three geographic grades to the polygon resulting of the convex hull of the presence data. MaxEnt models were performed using 70% of the presence data as training, with default settings and 10 replicates, and logistic output were converted as binary maps using the minimum training presence and summarized to show coincidence areas of the replicates. Models were evaluated with NicheToolsBox tool (http://shiny.conabio.gob.mx:3838/nichetoolb2/) to determine if predictions were effectively different from a random one (Peterson et al. 2008).

## Results

### *Mazama temama* (Kerr, 1792)

**New records.** COLOMBIA – **Department of Nariño** • Municipality of Consacá, "Vereda" Cariaco Bajo, buffer zone of the Santuario de Flora y Fauna Galeras; 01.1787°N, 077.4619°W; 1700 m alt.; 01.IX.2018; Luis G. Lasso, LGL 071 leg.; ♂ adult male, skull, forefeet, and fragments of the skin; GenBank: MW880928; MHN-UCa-M 1859 (Fig. 1A) • **Department of Nariño** • Municipality of Consacá, Vereda San Rafaél, Santuario de Flora y Fauna Galeras; 01.1661°N, 077.4442°W; ~2000 m alt.; 01.III.2011; Carola Lara, leg.; ♀ female, photographs alive (Fig. 1B).

**Identification.** A slender deer, reddish brown on the back with more grayish brown on neck, head, and hind and forefeet. The back is slightly bent and the rump is visibly high compared to the shoulders (Bello-Gutiérrez et al. 2010). The forehead has a tuft of long hair with dark ends. The skull is broad. The antlers are short (65.87 mm) and slightly curved. Antler length in males is approximately 50–96 mm (Groves and Grubb 2011). Other sympatric

**Table 2.** GenBank accession numbers for the cyt-b gene sequences used in this study. Accession numbers of sequences generated in this study are indicated in boldface type; all others were previously published and downloaded from GenBank.

| Taxon | Accession numbers |
|---|---|
| ***Mazama temama*** | **MW880928 (MHN-UCa-M 1859 Nariño-Colombia)** |
| *Mazama temama* | KP954716-KP954721; KC146956; KC146958; KY928661 |
| *Mazama temana* (identified in GenBank as *Odocoileus virginianus*) | JN632673 (Cundinamarca-Colombia) |
| *Odocoileus virginianus* | KY928662; KY928668; JN632671 |
| *Odocoileus hemionus* (Rafinesque, 1817) | FJ188751 |
| *Odocoileus hemionus* | FJ188881 |
| *Mazama bororo* Duarte, 1996 | DQ789187 |
| *Mazama nana* (Hensel, 1872) | DQ789227 |
| *Mazama americana* | DQ789220; DQ789230 |
| *Mazama rufina* | LT546656- LT546658; NC_020721; KR107035; KR107038-KR107040 |
| *Mazama nemorivaga* (F. Cuvier, 1817) | MN792634; MN792635; KY928658 |
| *Mazama gouazoubira* (G. Fischer, 1814) | NC_020720; KY928656 |
| *Alces alces* (Linnaeus, 1758) | NC_020677 |
| *Capreolus capreolus* Linnaeus, 1758 | NC_020684 |
| *Hydropotes inermis* (Swinhoe, 1870) | JN632649 |

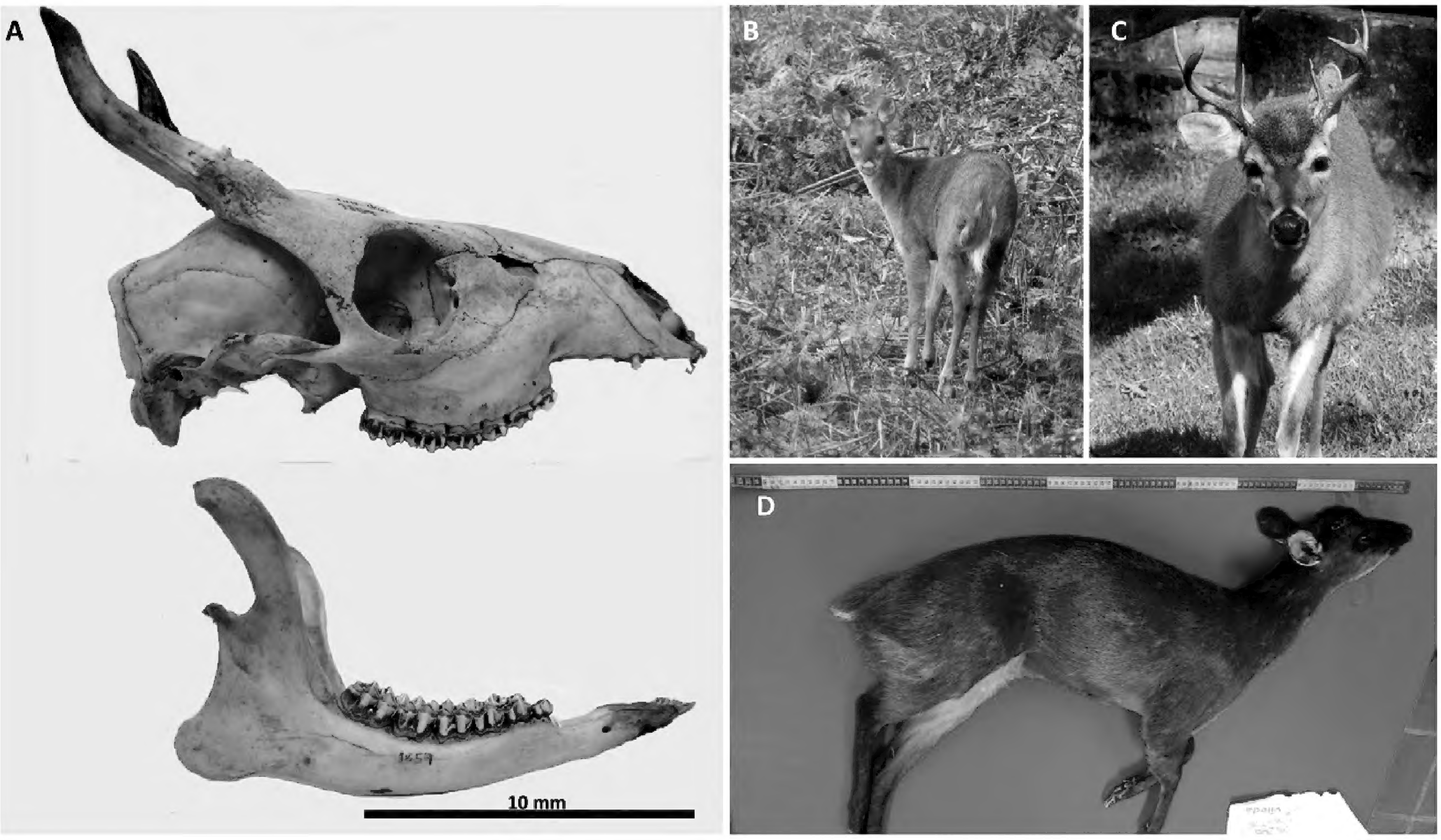


**Figure 1. A.** Lateral view of the skull of an adult male *Mazama temama* (MHN-UCa-M 1859; condylobasal length: 183.9 mm), from Vereda Cariaco Bajo, Municipality of Consacá, Department of Nariño, Colombia. **B.** Photograph of a live *M. temama* individual taken from Galeras Flora and Fauna Sanctuary, Department of Nariño, Colombia. **C.** Adult male *Odocoileus* sp. from the Central Andes of Colombia; note the branched antlers. **D.** Adult male *Mazama rufina* from the Central Andes of Colombia (MHN-UCa-M 3345); note the darker coloration, the black coloration on rostrum, fore and hindfeet, and smaller size than *M. temama*.

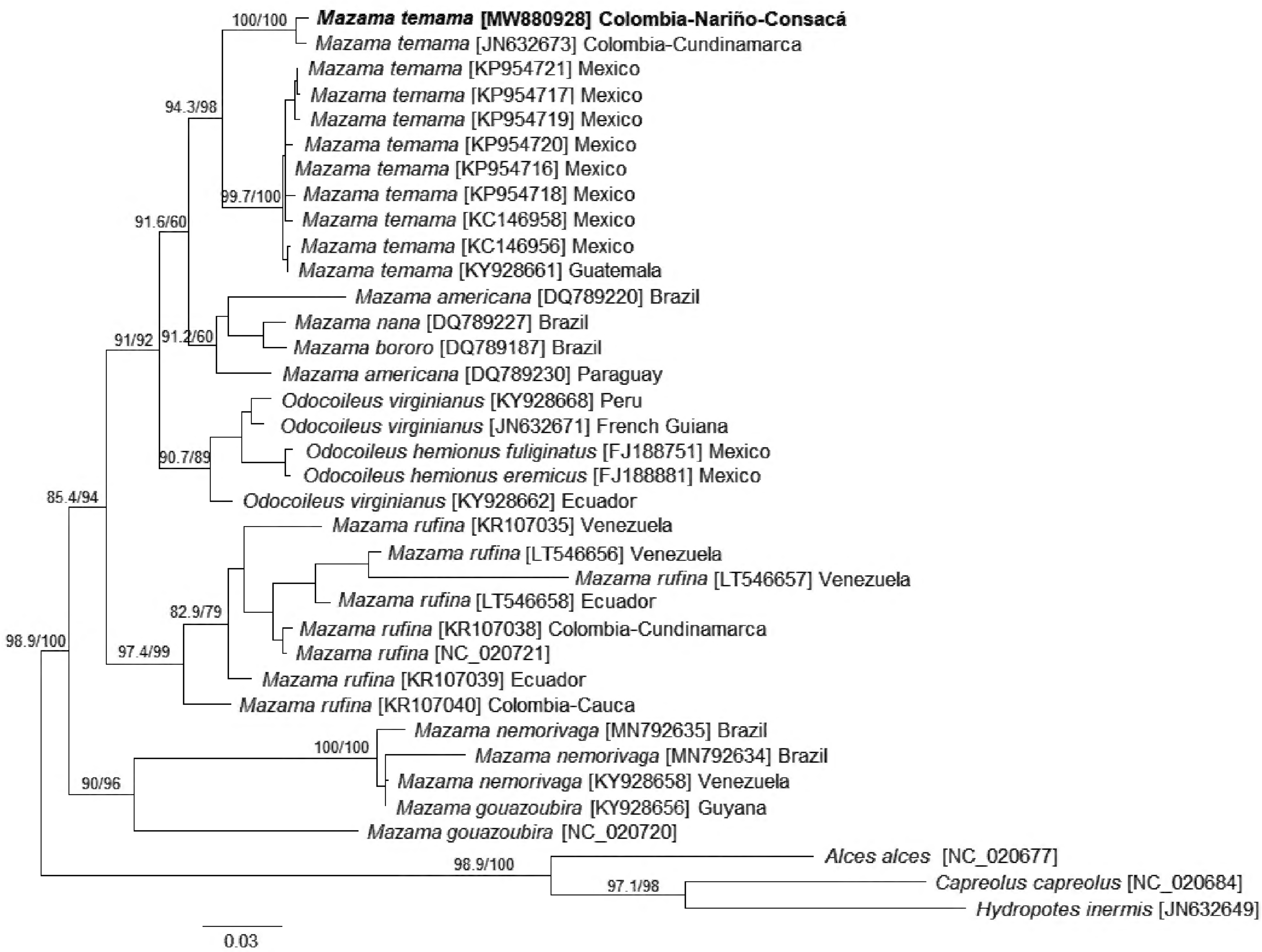


**Figure 2.** Maximum likelihood phylogenetic tree reconstruction based on a 849 bp fragment of the mitochondrial cyt-b gene of deer specimens using the TIM2+I+G4+F nucleotide substitution model. Values at nodes represent ultrafast bootstraps values and Shimodaira–Hasegawa–like approximate likelihood-ratio test (SH-like aLRT), respectively.

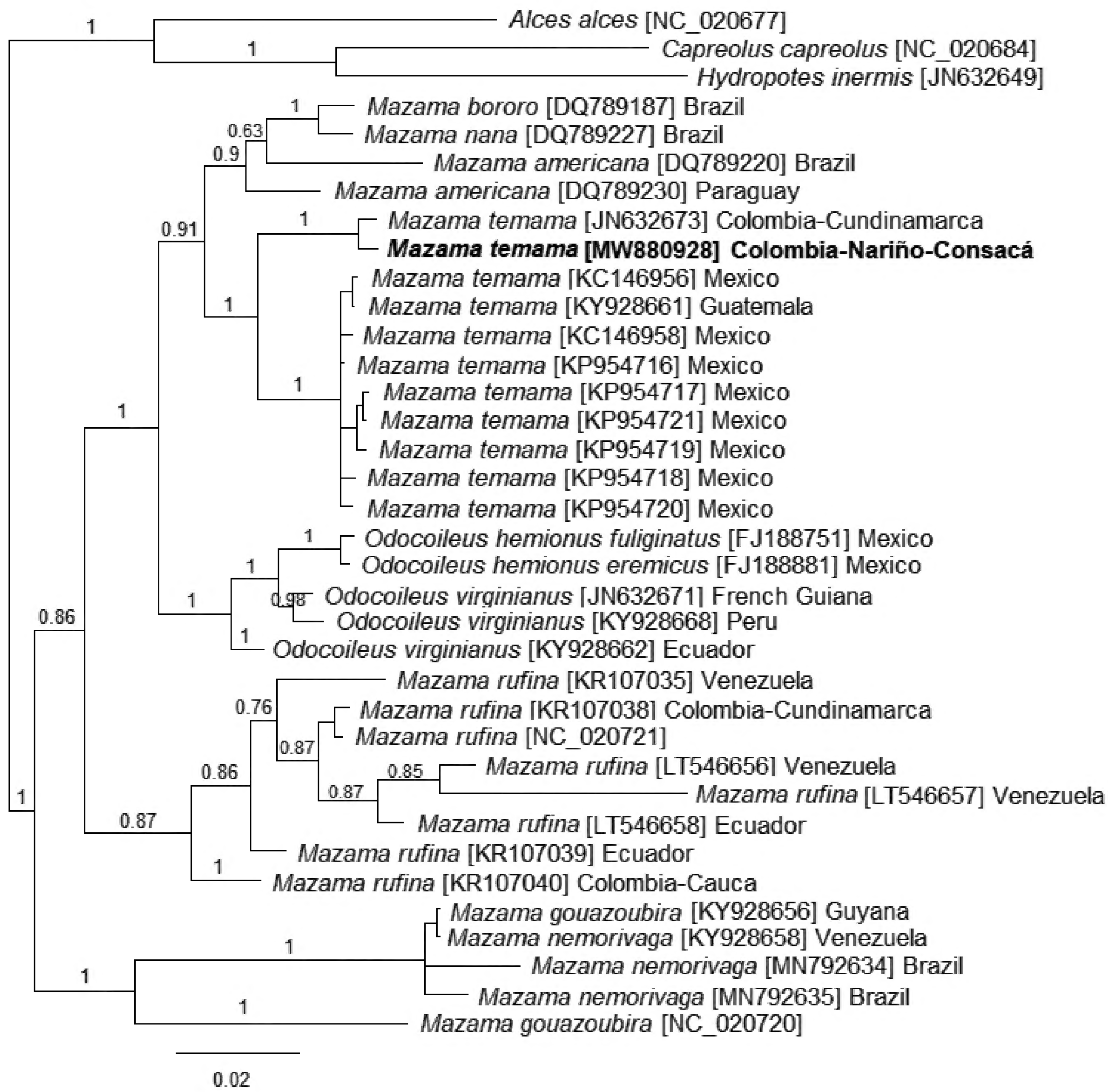


**Figure 3.** Phylogenetic tree based on an 849 bp fragment of the mitochondrial cyt-b gene of deer specimens, obtained by Bayesian inference (BI) using the GTR+F+G4 substitution model. Numbers above the nodes correspond to Bayesian posterior probabilities.

species from mid to highland elevations found in Colombia (Fig. 1C, D) are *Odocoileus* sp. which have branched antlers, and *Mazama rufina* (Pucheran, 1851) with smaller body size and skull (CBL: 145–159 mm) and has a narrower and substantially deeper lacrimal fossa (variable in *M. temama*), with darker fur on rostrum. Our specimen is also smaller in all cranial measurements than *M. americana* (Erxleben, 1777) (Cifuentes-Rincón et al. 2020), which has bigger body size (Table 1) and more reddish pelage.

The BLAST query recovered sequences from GenBank with similarity of 99.17% (accession number JN632673) and 95.36% (accession numbers KC146956, KC146958, KY928661). The origin of the samples was Colombia (JN632673, Department of Cundinamarca, but the locality is questionable), Mexico (KC146956, KC146958), and Guatemala (KY928661), all of them identified as *M. temama* (Escobedo-Morales et al. 2016; Gutiérrez et al. 2017). The genetic distances between Colombian sequences in respect to Mexican and Guatemalan sequences are 4.6 and 5.4 %, respectively (Table 3; Figs. 2, 3).

Our species distribution models showed an average AUC ratio of 1.7 and $p < 0.001$, suggesting a predictive power far from random. The majority of them (up to seven of 10 replicates) predict potential distribution areas within Colombia through the western slope of the Cordillera Occidental. The new records presented here belong to an area where average matches within one geographic degree ratio showed an approximate value of four. Overprediction areas seem to predict the occurrence of this species beyond the eastern slope of the Andes (Fig. 4).

## Discussion

Our *Mazama temama* records extend the southernmost

**Table 3.** Average intraspecific (on the diagonal) and interspecific (below the -) distances based on *p*-distances for cyt-b sequences.

| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 ***Mazama temama* (accession MW880928; Nariño, Colombia)** | - | | | | | | | | | | | | |
| 2 *Mazama temana* identified as *Odocoileus virginianus* (accession JN632673; Cundinamarca, Colombia) | 0.008 | - | | | | | | | | | | | |
| 3 *Odocoileus virginianus* | 0.065-0.074 | 0.059-0.068 | 0.011-0.026 | | | | | | | | | | |
| 4 *Odocoileus h. fuliginatus* | 0.071 | 0.068 | 0.025-0.038 | - | | | | | | | | | |
| 5 *Odocoileus h. eremicus* | 0.075 | 0.071 | 0.024-0.037 | 0.005 | - | | | | | | | | |
| 6 *Mazama temama* | 0.046-0.052 | 0.046-0.054 | 0.056-0.080 | 0.070-0.075 | 0.073-0.078 | 0.001-0.010 | | | | | | | |
| 7 *Mazama bororo* | 0.067 | 0.067 | 0.054-0.072 | 0.064 | 0.069 | 0.053-0.056 | - | | | | | | |
| 8 *Mazama nana* | 0.068 | 0.066 | 0.055-0.071 | 0.068 | 0.073 | 0.051-0.057 | 0.016 | - | | | | | |
| 9 *Mazama americana* | 0.062-0.081 | 0.063-0.081 | 0.050-0.074 | 0.062-0.073 | 0.064-0.076 | 0.050-0.073 | 0.039-0.055 | 0.038-0.054 | 0.052 | | | | |
| 10 *Mazama rufina* | 0.056-0.118 | 0.045-0.116 | 0.052-0.118 | 0.071-0.123 | 0.074-0.125 | 0.057-0.123 | 0.067-0.116 | 0.065-0.112 | 0.063-0.118 | 0.005-0.103 | | | |
| 11 *Mazama nemorivaga* | 0.117-0.130 | 0.119-0.133 | 0.104-0.133 | 0.123-0.133 | 0.124-0.133 | 0.102-0.122 | 0.098-0.113 | 0.094-0.116 | 0.090-0.112 | 0.063-0.123 | 0.012-0.025 | | |
| 12 *Mazama gouazoubira* | 0.118-0.130 | 0.113-0.120 | 0.102-0.119 | 0.117-0.123 | 0.120-0.124 | 0.109-0.121 | 0.113-0.115 | 0.116 | 0.082-0.114 | 0.081-0.123 | 0.001-0.107 | 0.107 | |
| 13 *Alces alces* | 0.123 | 0.124 | 0.108-0.122 | 0.132 | 0.133 | 0.122-0.133 | 0.124 | 0.123 | 0.115-0.126 | 0.106-0.130 | 0.122-0.132 | 0.125-0.132 | - |

geographic range of this species by approximately 300 km from the closest localities in Colombia (Montenegro et al. 2019). Furthermore, our species distribution models suggest the likely presence of this species in Ecuador (Fig. 4). The cyt-b sequence generated here also confirms the presence of the species in Colombia (Figs. 2, 3), as suggested in previous studies (Hassanin et al. 2012; Gutiérrez et al. 2017). In addition, this is only the second cyt-b sequence generated from any *M. temama* specimen from South America and the only one with a voucher specimen properly deposited in a museum collection (MHN-UCa-M 1859). The previous cyt-b record from Colombia did not have a voucher specimen and was misidentified as belonging to *Odocoileus virginianus* (Zimmermann, 1780) (Hassanin et al. 2012), but our phylogenetic reconstructions cast no doubt on its assignment to *M. temama* as suggested by Escobedo-Morales et al. (2016) and Gutiérrez et al. (2017). The morphometric data obtained from our voucher specimen also confirms this taxonomic designation, as the range of variation of the cranial measurements also falls within the range of specimens from Central America available in the literature (Allen 1916; Bello-Gutiérrez et al. 2010).

Our records also confirm the presence of *M. temama* in the Department of Nariño where other cervids such as *Mazama americana* have been previously documented (Ramírez-Chaves et al. 2010). However, *M. americana* has been recently restricted to Brazil and French Guiana (Cifuentes-Rincón et al. 2020). The distribution limits of *M. temama* in Colombia are still preliminary and require additional records. Our predictive models suggest that climatic conditions in the Nariño region could be a marginal habitat for the species. Additionally, we consider this contribution as a first step towards the revision of the taxonomy, systematics, and biogeography of cervids of Colombia. Finally, we also suggest the need for new integrative assessments of the diversity of cervids in Colombia to clarify the diversity and threats that this charismatic group of mammals face in this country.

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## References

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. Journal of Molecular Biology 215: 403–410.

Bello J, Reyna R, Schipper J (2016) *Mazama temama*. The IUCN Red List of Threatened Species 2016: e.T136290A22164644. https://doi.org/10.2305/iucn.uk.2016-2.rlts.t136290a22164644.en. Accessed on: 2021-5-0.

Bello-Gutiérrez J, Reyna-Hurtado R, Jorge H (2010) Central Ameri-

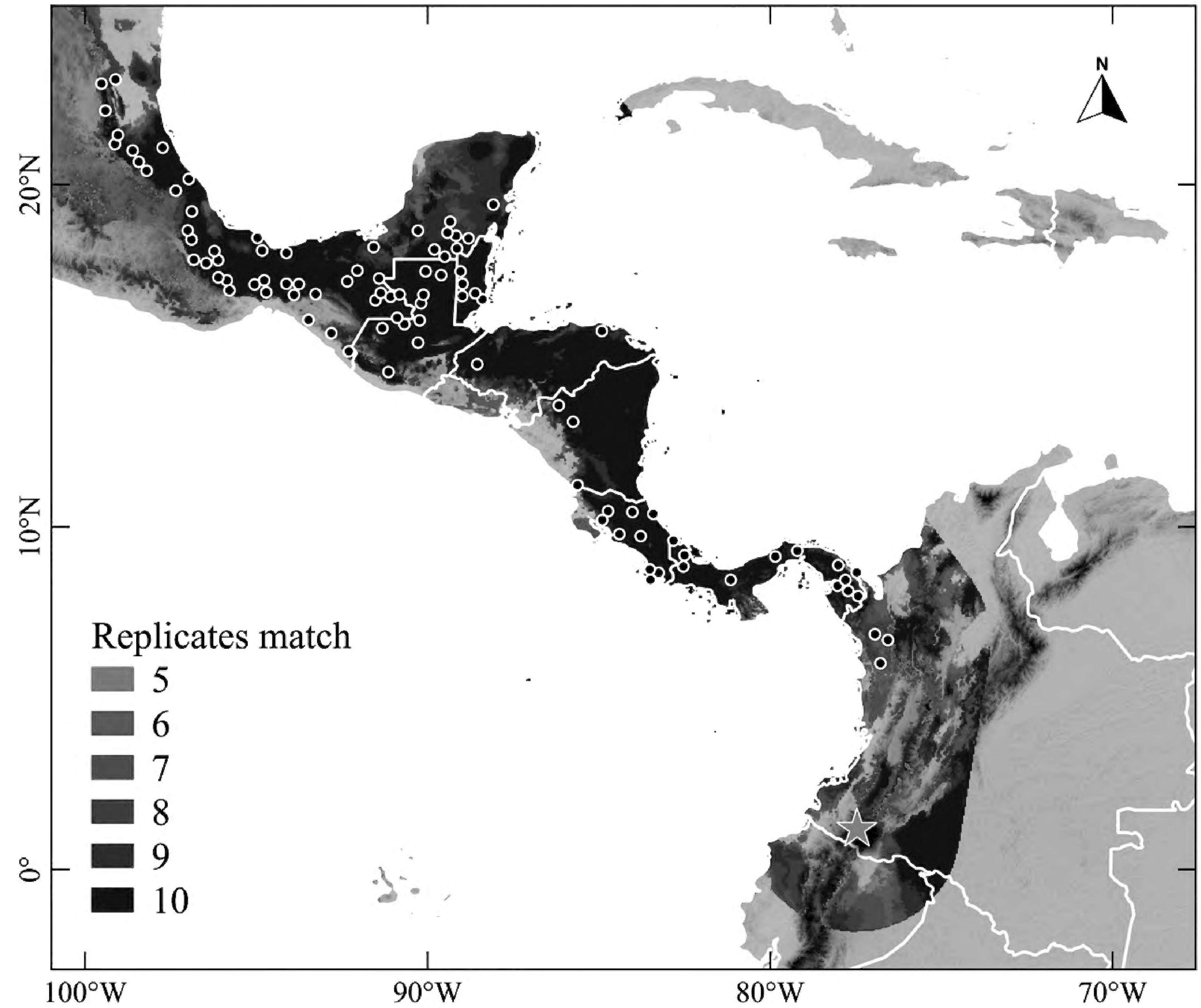


**Figure 4.** MaxEnt species distribution model of *Mazama temama*. New records in Colombia (red star) are based on one voucher specimen (MHN-UCa-M 1859) and photographs in this study. Additional localities are taken from literature and GBIF.

can Red Brocket Deer: *Mazama temama* (Kerr 1782). In: Duarte J, González S (Eds.), Neotropical cervidology: biology and medicine of Latin American deer. Funep/IUCN, Jaboticabal, 166–170.

Bickham JW, Patton JC, Schlitter DA, Rautenbach IL, Honeycutt RL (2004) Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). Molecular Phylogenetics and Evolution 33: 333–338. https://doi.org/10.1016/j.ympev.2004.06.012

Bickham J W, Wood CC, Patton JC (1995) Biogeographic implications of cytochrome b sequences and allozymes in Sockeye (*Oncorhynchus nerka*). Journal of Heredity 86: 140–144. https://doi.org/10.1093/oxfordjournals.jhered.a111544

Burgin CJ, Wilson DE, Mittermeier RA, Rylands AB, Lacher TW, Sechrest W (2020) Illustrated checklist of the mammals of the world. Lynx Ediciones, Barcelona, Spain, 1166 pp.

Cifuentes-Rincón A, Morales-Donoso JA, Sandoval EDP, Tomazella IM, Mantellatto AMB, de Thoisy B, Duarte JMB (2020) Designation of a neotype for *Mazama americana* (Artiodactyla, Cervidae) reveals a cryptic new complex of brocket deer species. ZooKeys 958: 143–164. https://doi.org/10.3897/zookeys.958.50300

Drummond AJ, Ashton B, Cheung M, Heled J, Kearse M, Moir R, Stones HS, Thierer T, Wilson A (2009). Geneious v8.14. http://www.geneious.com.

Duarte JMB, González S, Maldonado JE (2008) The surprising evolutionary history of South American deer. Molecular Phylogenetics and Evolution 49: 17–22. https://doi.org/10.1016/j.ympev.2008.07.009

Escobedo-Morales LA, Mandujano S, Eguiarte LE, Rodríguez-Rodríguez MA, Maldonado JE (2016) First phylogenetic analysis of Mesoamerican brocket deer *Mazama pandora* and *Mazama temama* (Cetartiodactyla: Cervidae) based on mitochondrial sequences: implications on Neotropical deer evolution. Mammalian Biology 81: 303–313. https://doi.org/10.1016/j.mambio.2016.02.003

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302-4315. https://doi.org/10.1002/joc.5086

GBIF.org (2021) GBIF occurrence download. https://doi.org/10.15468/dl.k86eb7

Gilbert C, Ropiquet A, Hassanin A (2006) Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): systematics, morphology, and biogeography. Molecular Phylogenetics and Evolution 40: 101–117. https://doi.org/10.1016/j.ympev.2006.02.017

Groves PC, Grubb P (2011) Ungulate taxonomy. Johns Hopkins University Press, Baltimore, USA, 309 pp.

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59: 307–321. https://doi.org/10.1093/sysbio/syq010

Gutiérrez EE, Maldonado JE, Radosavljevic A, Molinari J, Patterson BD, Martínez-C JM, Rutter AR, Hawkins MTR, Garcia FJ, Helgen KM (2015) The taxonomic status of *Mazama bricenii* and the significance of the Táchira Depression for mammalian endemism

in the Cordillera de Mérida, Venezuela. PLoS ONE 10: 1–24. https://doi.org/10.1371/journal.pone.0129113

Gutiérrez EE, Helgen KM, McDonough MM, Bauer F, Hawkins MTR, Escobedo-Morales LA, Patterson BD, Maldonado JE (2017) A gene-tree test of the traditional taxonomy of American deer: the importance of voucher specimens, geographic data, and dense sampling. ZooKeys 697: 87–131. https://doi.org/10.3897/zookeys.697.15124

Hassanin A, Delsuc F, Ropiquet A, Hammer C, Jansen Van Vuuren B, Matthee C, Ruiz-Garcia M, Catzeflis F, Areskoug V, Nguyen TT, Couloux A (2012) Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. Comptes Rendus - Biologies 335: 32–50. https://doi.org/10.1016/j.crvi.2011.11.002

Kalyaanamoorthy S, Minh BQ, Wong TKF, Von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14: 587–589. https://doi.org/10.1038/nmeth.4285

Kerr R (1792) The animal kingdom, or zoological system, of the celebrated Sir Charles Linnæus; being a translation of that part of the Systema Naturæ, as lately published, with great improvements, By Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copperplates. A. Strahan & T. Cadell, London, UK / W. Creech, Edinburgh, UK, 644 pp. https://doi.org/10.5962/bhl.title.57940

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35:1547–1549. https://doi.org/10.1093/molbev/msy096

Minh BQ, Nguyen MA, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30: 1188–1195. https://doi.org/10.1093/molbev/mst024

Montenegro OL, López-Arévalo HF, Mora-Beltrán C, Lizcano DJ, Serrano H, Mesa E, Bonilla-Sánchez A (2019) Tropical ungulates of Colombia. In: Gallina-Tessaro S (Ed.) Ecology and conservation of tropical ungulates in Latin America. Springer Nature, Champ, Switzerland, 157–194.

Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213: 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modeling 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips SJ, Dudík M, Schapire RE (2020) Maxent software for modeling species niches and distributions (Version 3.4.1). https://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on: 2020-1-07.

Rambaut A (2007) FigTree v1.4.3, A graphical viewer of phylogenetic trees. http://tree.bio.ed.ac.uk/software/figtree/.

Ramírez-Chaves HE, Noguera-Urbano EA (2010) Lista preliminar de los mamíferos (Mammalia: Theria) del departamento de Nariño, Colombia. Biota Colombiana 11: 117–140.

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Solari S, Muñoz-Saba Y, Rodríguez-Mahecha JV, Defler TR, Ramírez-Chaves HE, Trujillo F (2013) Riqueza, endemismo y conservación de los mamíferos de Colombia. Mastozoología Neotropical 20: 301–365.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X Windows Interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25: 4876–4882. https://doi.org/10.1093/nar/25.24.4876

Woodburne MO (2010) The Great American Biotic Interchange: Dispersals, tectonics, climate, Sea level and holding pens. Journal of Mammalian Evolution 17: 245–264. https://doi.org/10.1007/s10914-010-9144-8

Zhang D, Gao F, Jakovlić I, Zou H, Zhang J, Li WX, Wang GT (2020) PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. Molecular Ecology Resources 20: 348–355. https://doi.org/10.1111/1755-0998.13096